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ON THE OSTEOLOGY AND SYSTEMATIC POSITION OF THE ALCÆ.

DR. R. W. SHUFELDT.

SOME twelve or thirteen years ago I published several illustrated papers upon the osteology of the Alcæ, they having appeared in the *Journal of Anatomy* of London (Vol. XXIII, n.s.; Vol. III, October, 1888, pp. 1-39, Pls. I-V; January, 1889, pp. 165-186, Pls. VII-XI; April, 1889, pp. 400-427, Figs. 1-17 (text); July, 1889, pp. 537, 538, Figs. 1-8, and October, 1889, pp. 89-106, Pls. VI-VIII). In the text-figures and plates to these memoirs will be found reproductions of drawings of mine of the bones of a great many species of Alcæ, as *Alca torda*, *Plautus impennis*, *Uria* (two species), *Synthliborhamphus*, *Cepphus*, *Brachyrhamphus*, *Lunda*, *Fratercula*, *Cyclorrhynchus*, *Simorhynchus*, and others. In some cases several species of each are illustrated, there being upwards of one hundred figures in all. The descriptions are quite in detail, and taken in connection with the cuts and plates present accounts of nearly all the auks and puffins and their immediate allies known to science the world over. In fact, the only genera not thus treated are *Pseuduria*, *Micruria*, and *Ceratorhyncha*, and it is not likely that the osteology of any of these differs very much from that of known forms more or less nearly related to them, and certainly not to an extent to modify the present views of avian taxonomers upon the classification of the Alcæ. It will not, therefore, be necessary to reproduce much, if any, of that work in the present connection, and so far as the osteology of the extinct great auk (*Plautus impennis*) is concerned it has been very thoroughly described by numerous writers, and particularly by Sir Richard Owen and Mr. F. A. Lucas of the United States National Museum. To illustrate the present paper, however, I will offer a figure of the skeleton of the great auk, in order not

only to complete my series of illustrations of the skeletons of these birds, but also to bring before the readers of this paper the skeleton of a typical auk as a convenient reminder of the osteological characters of the bird forms here being considered. My space, therefore, will be principally occupied by a presentation of the various views of avian systematists on the position of the Alcæ in the system.

The auks and puffins, as is well known, constitute a very well circumscribed and distinct group of birds, with apparently no outlying forms, and, apart from *Plautus impennis*, no fossil remains of any species of them have as yet been discovered, or at least described. Dr. Sharpe records none in his *Hand-List of Birds* (1899, pp. 130-133).¹ Notwithstanding these facts, the opinions of the classifiers of birds are by no means unanimous on the question of the systematic position of the Alcæ. Professor Huxley, for example, grouped the Laridæ and the Alcidæ in one of his suborders, — the Cecomorphæ, — and said of the last-named family, "The Alcidæ in their pterylosis and other characters approach the penguins, especially through *Alca impennis*" (*Proc. Zool. Soc.*, 1867, p. 458); and Newton has remarked that "the affinity of the Alcidæ or auks (and through them the divers or Colymbidæ) to the gulls may be a matter beyond doubt, and there appears to be ground for considering them to be the degraded offspring of the former; but to the present writer it appears questionable whether the grebes (Podicipedidæ) have any real affinity to the two families with which they are usually associated; and this is a point deserving of more attention on the part of morphologists than it has hitherto received" (*Encycl. Brit.*, 9th ed., Vol. XVIII, art. "Ornithology," p. 45). Garrod, later on, who certainly entertained very peculiar notions about

¹ As this article goes to press I would say that a part of a fossil bone of an auk has been received by Mr. Lucas of the United States National Museum from a party in California, where it was found. This specimen I have been permitted to personally examine. It consists of the proximal moiety of a humerus that belonged to a species apparently as large as *Plautus*, but exhibiting even a more feeble development of the pectoral limbs. Mr. Lucas has described this specimen before the Biological Society of Washington, D.C., and his description will be published later on.

the affinities of birds, arrayed his Order IV, the Charadriiformes, between his Ciconiiformes (Order III) and his subclass Anomalogonatae (Order I, Piciformes). The Charadriiformes were made to contain two cohorts (α and β), namely, the Columbæ and the Limicolæ, the latter being represented by the Charadriidæ, the Gruidæ, the Laridæ, and the Alcidae. When one considers the birds he grouped in his Ciconiiformes and his Piciformes, such a classification is surely to be regarded more in the light of a taxonomical curiosity than to be taken seriously as a contribution to the *natural* classification of birds (cf. *Proc. Zool. Soc.*, 1874, p. 116).

As to the view entertained by Mr. W. A. Forbes on the position of the Alcæ, I have a number of letters from him on the subject, written to me from London, just before he left on his fatal trip to Africa, in which this question is referred to and set forth. These will be published in another connection by the present writer, together with others on various scientific matters of interest. Forbes's classification of birds was written out by him in his diary only four days before his death on the Niger, but it is more or less fragmentary, and I shall not discuss it here (cf. *Ibis*, 1884, p. 119).

Dr. P. L. Scater, in his classification of birds, places the two families Colymbidæ and Alcidae as alone constituting the group Pygopodes (Order XXI), inserting them in his scheme between the Tubinares and Impennes (Orders XX and XXII, respectively). (See *The Ibis* for 1880.) This is certainly at variance with Professor Huxley's views, though, as Dr. Scater's Order XIX (Gaviæ) includes only the Laridæ, it agrees in one way with what Professor Huxley proposed, and that is, that the Laridæ, the Procellariidæ, the Colymbidæ, and the Alcidae, grouped as families, were next nearest the penguins in their affinities.

Dr. Reichenow (1882) surely did not appreciate the value of the osteological characters of the Impennes (penguins) when in his scheme of classification for Aves (*Die Vögel der Zoologischen Gärten*) he placed the Spheniscidæ, the Alcidae, and the Colymbidæ as the three families constituting his second order, the Urinatores. Such an arrangement distinctly differs

from that of Huxley and others, and cannot be sustained upon morphological grounds, which are the only true ones to be considered in the natural classification of animals of any kind. Coues and Ridgway, as representative authorities of the American Ornithologists' Union (1884-95), consider the Alcidae to be a family of the order Pygopodes, arrayed with the Urinatoridae in a suborder, Cepphi. Why a grebe (*Æchmophorus*) and a puffin (*Lunda*) should, as birds, be associated in the same order, is quite beyond the comprehension of the present writer, who believes that Professor Cope went equally wide of the mark when, in his classificatory scheme for Aves, he made an order, Euornithes, which is included in his superorder Eurhipiduræ; and in the former, the Alcidae fall within the suborder Cecomorphæ (cf. *Amer. Nat.*, October, 1889).

The late Professor William Kitchen Parker, in his admirable memoir *On the Morphology of the Duck and Auk Tribes*, says, on page 91: "I am under the impression that penguins never possessed quills, and that their adaptation to aquatic life and their great power of diving took place much earlier in their ancestral history than in the case of the auks and guillemots—birds that tend to become a sort of palearctic penguin but never quite lose the marks of their former adaptations to a more terrestrial life. I conceive of their ancestors in amphibious or limicolous birds, and I imagine the forefathers of gulls, plovers, rails—the auk tribe—as being very much alike and very nearly related. . . . All the penguins are alike in everything that is important; of the Alcidae only one, *Alca impennis*, became transformed into the likeness of a penguin; the specialization of the family has been imperfect as compared with the penguins, and, as I believe, took place later in time" (*Cunningham Memoirs*, No. VI, Royal Irish Academy, Dublin, November, 1890).

A marked approach toward a natural classification of the several groups of birds I have been considering here was arrived at when Dr. Leonard Stejneger published his scheme in 1885 (*Standard Natural History*, Boston). In it the

arrangement proposed by this keen observer of morphological characters in animals is, in the case of the birds in question, as follows:

SUPERORDER	ORDER	SUPERFAMILY	FAMILY
(II) Impennes	(V) Ptilopteri	Colymboideæ	Spheniscidæ
		Heliornithoideæ	Colymbidæ
			{ <i>Heliornis</i>
			{ (Heliornidæ)
(III) Euornithes	(VI) Cecomorphæ	Alcoideæ	{ Urinatoridæ
			{ Alcideæ
		Laroideæ	{ Stercorariidæ
			{ Laridæ
		Procellaroideæ	{ Diomedidæ
			{ Procellaridæ
			{ Pelecanoididæ

From this it will be seen that the penguins (Spheniscidæ) are well separated from the grebes (Podicipedidæ: *auct.*) and these latter from the loons and auks, an arrangement which is a very natural one, based as it is upon an appreciation of the structural characters of the representatives of the families considered. Still, in the opinion of the present writer the association of the Urinatoridæ and the Alcideæ is too close, and not warranted upon morphological grounds.

Several years later, Dr. Hans Gadow (*Proc. Zool. Soc.*, 1892, p. 229) also proposed a "Classification of Birds," in which he attempted to employ all the known structural characters of the class Aves, as well as the previous opinions of all recognized authorities upon avian taxonomy. His position selected for the Alcæ is shown in the following scheme, abstracted from his arrangement as a whole:

16. Charadriiformes	I. Limicolæ	{ Chionididæ
		{ Charadriidæ
		{ Glareolidæ
		{ Thinocoridæ
		{ Œdicnemidæ
		{ Parridæ
	II. Gaviæ	{ Alcideæ
		{ Laridæ

In this scheme Dr. Gadow includes *Attagis* in the *Thinocoridae*, and very widely separates the *Charadriiformes*, as constituted above by him, from the *Sphenisciformes* (8 of his scheme) and the *Procellariiformes* (9 of his scheme),—these last two groups having the *Ardeiformes* (10), the *Falconiformes* (11), the *Anseriformes* (12), *Crypturiformes* (13), *Galliformes* (14), and *Gruiformes* (15), standing between the *Colymbiformes* (7) and the aforesaid *Charadriiformes* (16). In other words, the loons and grebes are separated in this lineal arrangement from the group containing the auks and gulls, by the groups containing the penguins, the *Tubinares*, the *Steganopodes*, the herons, the *Cathartidae* and *Accipitres*, the *Crypturi*, the fowls, and the *Gruiformes*.

This curious arrangement has doubtless been produced by the way in which the structural characters have been employed and contrasted. The entire scheme is highly unnatural in many particulars, as, for example, the relations indicated for the flamingoes to the storks, the two families alone representing the *Pelargi*, and this last group being associated with the herons and *Steganopodes* in an order, *Ardeiformes*. Between this last and the order *Anseriformes* stands the order *Falconiformes*, thus giving not the slightest suggestion as to the undoubted relation of the flamingoes to the anserine birds. This comes of the danger of using too many structural characters, and those characters of very different values and weight, and not properly contrasted. Such a practice will be sure to lead one away from the correct solution of the true relationships existing among birds in nature, taking the group as a whole, both existing and extinct, since birds were birds at all, in time;—and it is the expression of this in a taxonomic scheme of some sort or other that really we all are so desirous of perfecting. Sometimes, too, even the *lineal* scheme of so high an authority as Dr. Max Fürbringer is open to the same criticism, but not so when we come to examine the famous “avian tree” he constructed for us, and published in his great classic on the subject, *Untersuchungen zur Morphologie und Systematik der Vögel*, in 1888. With respect to the *Alcae*, in

his lineal arrangement Professor Fürbringer classifies the family Alcidae as follows :

Charadriornithes (Ægialornithes)	Charadriiformes	Laro-Limicolæ	Charadrii	{	Charadriidæ
				{	Glareolidæ
					Dromadidæ
					Chionididæ
					Laridæ
					Alcidæ
					Thinocoridæ
		Parræ			Parridæ
		Otides		{	(Edicnemidæ
					Otididæ

The relationships are exhibited more naturally in his “Phylogenetic Tree,” where the offshooting of the various groups and subgroups can be much better appreciated, as they are, too, in the several sectional projections of the “Tree” he has given us.

Finally, passing over the several attempts of the late Mr. Henry Seebohm to classify the class *Aves* in so far as orders and suborders are concerned, and the earlier provisional schemes of Dr. R. Bowdler Sharpe, I come to the last one of the latter eminent authority as set forth in his *Hand-List of Birds*, published by the British Museum in 1899 (Vol. I, p. 130).

In this scheme the following arrangement has been proposed :

ORDERS	FAMILIES	SUBFAMILIES		
XII. Procellariiformes	{	{	Procellariidæ	Procellarinæ
			Oceanitinæ	
			Puffinidæ	Puffininæ
			Fulmarinæ	
	{	Pelecanoididæ		
{	Diomedeidæ			
	<i>Incertæ Sedis</i> . .	(Hydrornis)		
XIII. Alciformes . .	Alcidæ	{	Alcinæ	
			Fraterculinæ	
XIV. Lariformes . .	{	{	Laridæ	Sterninæ
			Rhynchopinæ	
			Larinæ	
			Stercorariidæ	
	<i>Incertæ Sedis</i>	(Halcyornis)		

There is a great deal to be said in favor of this classification, and it can be largely supported when the osteological characters presented on the part of the bird forms representing these various families are taken into consideration, as I have already demonstrated in my memoirs in the *Journal of Anatomy and Physiology* of London cited in a former paragraph of this paper. Dr. Sharpe is also quite correct when he places, as he does, in *The Hand-List of Birds* these three orders between the Charadriiformes upon the one hand and the Sphenisciformes upon the other.

Synopsis of the Osteological Characters of the Alcæ.

1. The superior mandible of the skull varies in its morphology. It may have its anterior portion elevated, convex, prominent, laterally compressed, and cultrate, terminating in a sharp hook, as in *Alca*, *Fratercula*, and *Lunda*; or, the superior mandible may not be hooked, the foregoing characters remaining the same, as in *Cyclorhynchus*; or, it may taper gradually to a point, with the culmen roundly convex and not modified, as in *Synthliborhamphus*, *Brachyrhamphus*, *Cephus*, and in *Uria*; or, finally, it may be broad at its base, and shortened, while its general characters remain the same.

2. With regard to the *supraorbital glandular depressions*, they may be entire, the upper orbital rim being finished off with an osseous emargination; and this associated with the *crotophyte fossæ* either reaching the supraoccipital prominence or encroaching upon its summit, as in *Alca* and in *Uria*; or, the supraorbital glandular depressions may not be entire, the upper orbital rim being absorbed, producing wing-like post-frontals, and these characters associated with lateral *crotophyte fossæ*, as in *Fratercula*, *Lunda*, *Simorhynchus*, *Ptychorhamphus*, *Synthliborhamphus*, *Brachyrhamphus*, and *Cephus*. (It is in *Brachyrhamphus* that the *crotophyte fossæ* are lateral.)

3. The extent to which the *interorbital septum* and the anterior wall of the brain-case ossifies varies greatly with age and is therefore an unreliable character. There is always more or less bony deficiency in these parts in the *Alcæ*.

In *Cyclorrhynchus psittaculus* the maxillo-palatines are nearly horizontal, while in *Lunda* they are nearly vertical, the angle for these bones varying between these two planes for the different genera, they having an obliquity of about 45° in *Alca* and *Uria*. The *vomer* also varies; in *Alca* and *Uria* it is never produced as a spine in front, while this is its normal condition in *Simorhynchus* and the Auklets generally. In certain *Fraterculinæ* it varies between these two extremes.

4. The *mandible*, though varying not a little throughout the group, presents in its general form the same fundamental characters in all. The angle is always recurved, the surangular is pierced by one large foramen, or two small ones; the ramal vacuity is usually closed by the splenial or dentary, and the sides of each ramus are more or less vertical, and the symphysis comparatively short. It is V-shaped when viewed from above.

5. As a rule, the Alcæ have the first pair of small free ribs on the fourteenth vertebra, followed by a better developed free pair on the fifteenth. In *Brachyrhamphus* and *Synthlorbhamphus*, the first pair of free riblets may be found on the thirteenth vertebra. Again, the number of ribs reaching the sternum through costal ribs varies, the variance depending upon a greater number of posterior pairs in some of the species. As we pass from the typical auks to the puffins the number of pairs of ribs decrease; for instance, *Alca torda* has *nine* pairs posterior to the first two free pairs, eight of which articulate with costal ribs, and they become long and sweeping behind. *Lunda cirrhata*, as a rule, has but *seven* corresponding pairs, and only six of these articulate with costal ribs; and they are comparatively shorter and less sweeping.

6. The *pelvis* offers us no definite characters that can be relied upon as constant, beyond the gradual change in its form. It is long and narrow in *Plautus*, *Alca*, and *Uria*, to become shorter and more spreading posteriorly as we pass to other genera.

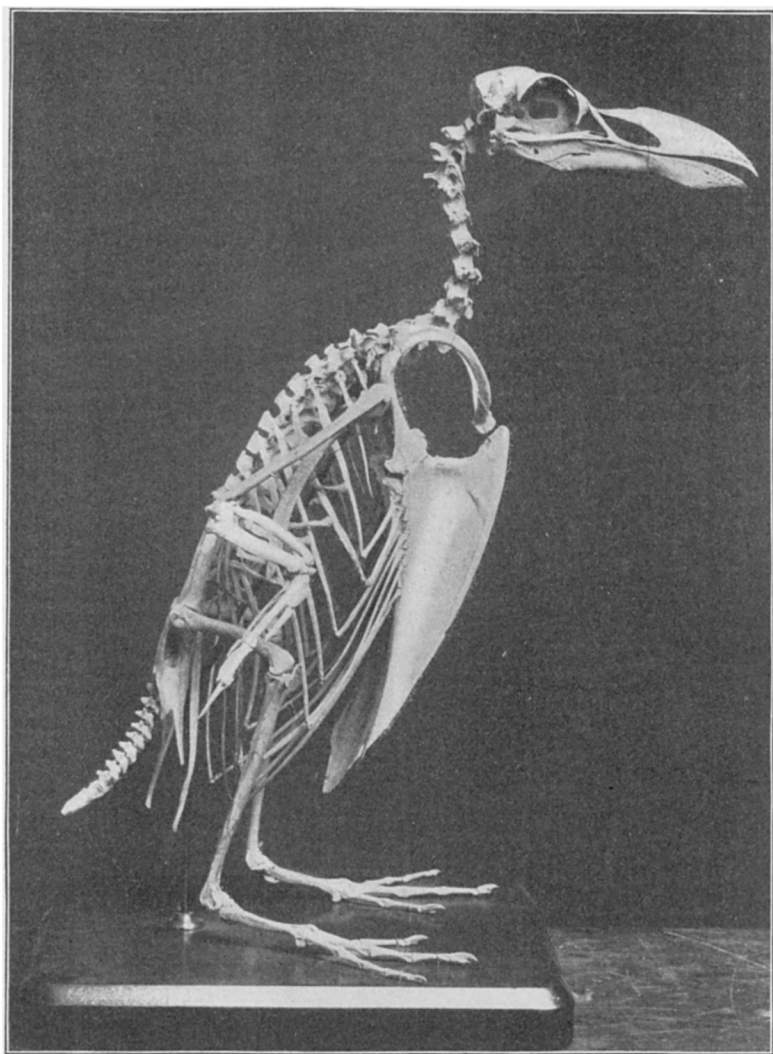
7. The number of free *caudal vertebræ* range from seven to ten, not including the pygostyle. I have found the latter number in a specimen of *Lunda cirrhata*.

8. When the xiphoidal extremity of the *sternum* is notched, it is 1-notched upon either side, but this is a very variable

character among the Alcæ. In some sterna a *small foramen may occur upon one side only*, and even this may be absent. Between these extremes a great variety of patterns is to be met with, as a notch upon one side and a foramen on the other, or both foramen and notch upon either side. The sternal body is long and narrow in Alca, Uria, Synthliborhamphus, Brachyrhamphus, and in the extinct Plautus — those species, on the other hand, in which the sternum has a single notch on either side, and a single foramen within its inner border, the sternal body is rather broader anteriorly and more spreading behind, as in Cepphus, Lunda, and Fratercula. In Simorhynchus the sternum, having the same fundamental pattern, is long and narrow, with the xiphoidal extremity much produced beyond the carinal termination, being swelled and concave above and with one large, oblique, elliptical *foramen* on either side. This character also varies for different genera and species. The skeletons of the limbs do not appear to offer any constant characters. Full descriptions of the morphology of these parts, as well as the various forms of the sternum, are given in my previous memoirs, and they are illustrated by numerous cuts and figures, both in the text and on the plates.

On the Systematic Position of the Alcæ.

The Alcæ constitute a suborder of birds, in which is included but the single family Alcidæ. This family may be conveniently divided into two subfamilies, — the Alcinæ, containing all the true auks, and the Fraterculinæ, containing the puffins. As a group the Alcæ are connected upon the one hand with the Limicolæ through the Longipennes; in other words, to the great snipe-plover group, and their allies through the gulls and their allies. On the other hand, they are connected with the Pygopodes and Impennes through the Tubinares, that is, through the petrel types with the penguins, the loons, the grebes, and their extinct allies, the toothed birds of the hesperornithine type of structure. Later on these relationships will be set forth in my scheme of classification of the class *Aves*, now in the course of completion.



EXPLANATION OF THE PLATE.

Skeleton of the Great Auk (*Plautus impennis*). Reduced. Coll. U. S. National Museum, No. 18,117. This skeleton is made up of the bones of numerous individuals.